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► To cite this version:

Gilles André, Sébastien Lavergne, Christopher Carcaillet. Unsuspected prevalence of *Pinus cembra* in the high-elevation sky islands of the western Alps. *Plant Ecology*, 2023, 224 (10), pp.865-873. 10.1007/s11258-023-01341-1 . hal-04255526

HAL Id: hal-04255526

<https://hal.science/hal-04255526v1>

Submitted on 24 Oct 2023

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1 Short Communication (max 2500 words)

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3 Unsuspected prevalence of *Pinus cembra* in the high-elevation sky islands of the western Alps

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19
20 # An unreviewed version of this article was freely archived in bioRxiv on 13 July 2020,
21 <https://doi.org/10.1101/2020.07.08.193300>

24 **Abstract (250 words)**

25 A survey of *Pinus cembra* (Arolla pine) growing above 2800 m elevation was conducted in an ecoregion of
26 the western Alps, where the highest treeline is at ~2650 m. The concepts of treeline and species line are
27 discussed based on these field observations. The species line is the biological limit of a species, with
28 inherited nested historical and current processes of high-mountain socio-ecosystems, while the treeline
29 strictly concerns the limit of erect trees. Arolla pines were located and described (height, physiognomy),
30 and their habitats recorded (elevation, slope, aspect). Individuals occurred up to 3200 m on east-facing
31 steep and rocky slopes, with density decreasing exponentially with increasing elevation (halving every 40
32 m). East-facing habitats benefit from the main atmospheric moisture coming from the east (Italy).
33 Individuals were mostly dwarf-shaped/prostrate (58%), or trees (39%; max height 3.8 m). They usually do
34 not bear female cones, and needles are smaller by half compared to those of pines growing in lower
35 elevation forests. Their morphology indicates harsh growing conditions due to elevation (aridity, frost) and
36 disturbances (wind, snow, rockfall). Habitat preference primarily on grass-free steep rocky slopes and cliffs
37 at high elevation is likely explained by the exclusion of livestock impacts (grazing, trampling). These pines
38 constitute noteworthy “sky island” populations. *Larix decidua* and *Pinus uncinata* were also recorded above
39 the treeline, but with lower maximum elevation and density than *Pinus cembra*. These observations
40 highlight a complex pattern of species treeline in the western Alps, and probably beyond, with relevance
41 to issues in conservation science.

42

43 Introduction

44 The altitudinal treeline has long been a topic of studies (Tranquillini 1979; Wieser and Tausz 2007),
45 notably because it is primarily climate driven (Körner 2021) and can be used as a climate proxy
46 (Kullman 1995). Treeline is often defined based on the physiognomy of plant rather than of species
47 occurrence, with physiognomy being a functional life trait (Körner 2012). The *treeline* concept
48 considers that plants must be erect and taller than a few metres (Payette 1983; Eronen and Huttunen
49 1993; Kašpar and Treml 2018), growing in woodland or tree-islands (Holtmeier and Broll 1992), or
50 even visible by remote sensing (Paulsen and Körner 2001; Gehrig-Fasel et al. 2007). Therefore, the
51 concepts of *treeline* and *species line* must be distinguished. The species line, which is less conservative,
52 is the ecological limit of a species regardless of its physiognomy and stand structure, while the *treeline*
53 concerns only the erect trees.

54 Tree physiognomy depends on the micro-scale environment that regulates plant physiology (Körner
55 2012). During their lifetime, trees can alternate between erect and prostrate (*krummholz*) stature, due
56 to variations in climate (eg, snow depth) altering the winter survival of meristems (Lavoie and Payette
57 1994; Brodersen et al 2019), or to changes in herbivory or parasitism (Körner 1998). Therefore, the
58 species line represents either a relic of stressed treeline with formerly erect trees potentially >100
59 years old (Laberge et al. 2001, Wurth et al. 2018), or the forefront of tree expansion due to the release
60 of stressors (Kullman 2001; Brodie et al. 2019), or a *status quo* of occasional and stochastic
61 recruitment above treeline. Indeed, tree height and shape are largely independent of age and result
62 from mechanisms that have affected plants during their lifetime; thus, small individuals are not
63 necessarily “seedlings”. Further, scattered trees can inherit features from non-climatic historical
64 factors, eg, domestic grazing (Carrer 2015) and anthropogenic burning (Carcaillet et al. 2022), that
65 may have excluded or hindered tree recruitment for centuries and, therefore lowered the treeline. If
66 individual physiognomy is, for a time, shaped by these historical factors, then the mere presence of
67 tree species — largely overlooked and underestimated (Oberg and Kullman 2011) — could be
68 considered part of the treeline, especially if the individuals are not growing in their best nutritional
69 habitat (gentler slopes, deeper soils) but in places that exclude domestic grazers (eg, rocky outcrops,
70 cliffs). Therefore, the treeline and its surroundings form a socio-ecosystem (Liu et al. 2007) resulting
71 from coupled natural and anthropogenic processes, including legacies of past conditions, producing
72 non-linear trends and patterns that are sometimes delayed.

73 In the European Alps, woody species show a current slight upward trend (Vitasse et al. 2021), largely
74 controlled by land use abandonment since at least the 1950s (Chauchard et al. 2010; Frei et al. 2023).
75 Above treeline, which typically occurs in the range 2100–2400 m above sea level (asl), the alpine belt
76 has been greening since the 1990s due to the expansion of denser herb cover and shrubs on north-

77 facing slopes and outcrops or in screes (Carlson et al. 2017; Choler et al. 2021). The present paper
78 reports a systematic census of high-elevation *Pinus cembra* L. (Arolla pine) growing above 2800 m asl
79 in a small area of the western Alps. The aim is to demonstrate that the conventional treeline of erect
80 individuals does not always capture the reality, which can differ significantly from species lines that
81 are generally ignored or understated. The survey area is large enough to allow a significant number of
82 observations and was conducted in an eco-region where *P. cembra* has previously been recorded up
83 to 2800 m asl (Bono and Barbero 1971; Motta and Nola 2001; Carcaillet and Blarquez 2019). Because
84 higher occurrences of *P. cembra* were also reported (André 2016), the lower threshold of 2800 m
85 appeared meaningful for the study. Elevation, slope and aspect, and rock cover are the main drivers of
86 pine occurrence and height (Motta and Nola 2001; Housset et al. 2021). We hypothesised that the
87 species-line for *P. cembra* should be higher on south-facing slopes (longer growing season) and on
88 gentler slopes with more developed soils (better water storage, nutrient availability).

89 These data, supplemented by more extensive data collected in the western Alps, contribute to a
90 discussion of the regional species line for *P. cembra* in light of past and current environmental
91 processes. With ongoing global warming and land use abandonment, pine outposts far above the line
92 of erect individuals provide suitable habitat nuclei for further successful establishment of individuals
93 dispersed from lower elevations (facilitation) or could be possible sources of pine expansion if climatic
94 conditions change sufficiently to allow in situ seed production. They could potentially contribute to the
95 greening of the alpine belt. This study seeks to contribute to the definition and framing of future
96 research on the ecology and biology of pines living considerably above the conventional treeline.

97 **Material and Methods**

98 **Study area**

99 The present study area comprises inner valleys and massifs in the western Alps, between 6.75°E-
100 7.15°E and 44.60°N-44.78°N (Figure 1). From west to east, the area covers the Queyras Massif and the
101 Guil Valley, France, and the Varaita Valley with the Mount Viso Massif, Italy (Supplementary Figure S1).
102 The survey area is assessed to encompass around 31 km² (Table S1).

103 In the western Alps, the treeline is considered to occur at nearly 2100-2200 m asl in the northern
104 massifs, and approximately 2300-2400 m in the southern ones. The treeline follows a clear gradient,
105 being lower in colder and wetter massifs (eg, Ecrins) than in warmer and drier massifs (eg, Queyras,
106 Mount Viso) at the same latitude. On the south-facing slopes of Mount Viso, the highest treeline was
107 reported up to 2650 m (Motta and Nola 2001) and scattered pines up to 2810 m (Bono and Barbero
108 1971; Motta and Dotta 1994).

109 **Study species**

110 *Pinus cembra* (Arolla pine) co-dominates the upper forests of inner valleys with *Larix decidua* Mill.,
111 and sometimes *Pinus uncinata* Ram. ex. DC or *Picea abies* (L.) H. Karst. It is a long-lived species
112 (>500 years) with long generation intervals and maintains stable population sizes over a long time
113 without inbreeding depression with high genetic variation (Gugerli et al. 2009; Toth et al. 2019). *Pinus*
114 *cembra* produces heavy seeds, dispersed only by a mutualistic bird (*Nucifraga caryocatactes* L.,
115 nutcracker), which specializes in caching nut-like seeds in the soil, up to hundreds of metres from the
116 source pine, as a winter food resource. This ornithochory strictly controls seed dispersion and shapes
117 colonization to specific landscape elements selected by nutcrackers. *Pinus cembra* interacts both with
118 fungi, symbiotic for nutrients and water acquisition, and pathogens (Merges et al. 2018). These
119 interactions with bird and fungi drive pine recruitment (Neuschulz et al. 2018).

120 **Data collection**

121 All observed occurrences of *Pinus cembra* above 2800 m elevation in the survey area were mapped
122 using GPS. Elevation, slope and aspect were recorded, and subsequently verified using online public
123 maps and satellite/aerial images on the Geoportail web site (geoportail.gouv.fr/) or the Google Earth
124 Pro program.

125 Plant height was measured, or visually estimated (± 10 cm) for individuals that were inaccessible.
126 Other data collected included the individual physiognomy, isolated *versus* clustered structure, and
127 environment (substratum, aspect and slope). At least one photograph was taken to support and
128 expand upon the description of stand contexts, habitats (rock cover, aspect, slope, etc.), and growth
129 form. Based on photographs, some clustered individuals could not be distinguished from each other
130 for growth form description, ie, 79 out of 544. Pine density was calculated as the number of
131 individuals per elevation or aspect class.

132 The aspect of high-elevation individuals/clusters recorded here was compared to the 1747 field
133 observations with aspect data among the 3100 containing *P. cembra* community relevés and habitat
134 descriptions, including geographical coordinates (all below 2800 m asl), from the botanical database of
135 the French National Alpine Botanical Conservatory (CBNA; www.cbn-alpin.fr/). Because the individual
136 density differed between the CBNA database and our data, and in order to graphically represent
137 aspect, the pine density per aspect class was min-max rescaled between 0 and 1 by subtracting the
138 minimum number per elevation class and dividing by the range of values of this class:

$$x'_i = (x_i - x_{min}) / (x_{max} - x_{min})$$

139 where x'_i is the rescaled pine number of x_i , and x_{max} and x_{min} are the maximum and minimum numbers
140 of pines per class, respectively.

141 Results

142 Elevation, habitat, slope and aspect

143 In total, 544 *Pinus cembra* were recorded above 2800 m asl in 24 stands (Supplementary Fig. S1).
144 The individual frequency decreased with site elevation, reaching a maximum elevation of 3200 m asl
145 (Fig. 2). The median pine elevation was 2835 m (mean \pm sd: 2853 \pm 58 m); 75% of all recorded
146 individuals occurred below 2870 m. The frequency distribution of pines across elevation classes was
147 negative exponential ($r^2 = 0.99$; Fig. 2), with a halving of individuals for every 40 m of elevation. While
148 *Pinus uncinata*, *Larix decidua* and *Picea abies* are also found in the inner valley treeline forests of this
149 region, *Larix* was encountered only infrequently above 2800 m (3 occurrences), and *P. uncinata* and *P.*
150 *abies* not at all.

151 Individuals of *P. cembra* were generally situated on steep (cliff) and rocky habitats, and on ridges.
152 The modal slope class was 50-60°. About 94% of all individuals were found on slopes between 40° and
153 70° (n = 511; Fig. 3a). Rarely, some pines grew with grasses, but always embedded between rocks or
154 within rocky outcrops in a grass-free habitat. In cliff habitat, individuals were rooted in cracks or
155 between bedrock layers, which offered a weathered mineral substrate (Fig. 4). Pines grew on
156 extremely heterogeneous bedrock, including dolomitic limestone (Fig. 4kl), calcareous sandstone (Fig.
157 4d), calc-schist, flysch, ophiolites (Fig. 4gh), basalt, quartzite (Fig. 4ij), acidic schist and sandstone,
158 demonstrating that the chemical quality of bedrock did not control their occurrence.

159 The modal aspect for pines above 2800 m was east and, ranged from northeast to southeast (Fig.
160 3b). When sorted by elevation and latitude and clustered by percentile, all pines located below
161 2870 m (75th percentile) were on slopes facing east to northeast. In contrast, the upper quartile of
162 individuals, situated between 2870 to 3200 m, mostly faced southeast, and when considering only the
163 95th percentile (n = 27, 2960-3200 m), they were all facing southeast. These aspect patterns are
164 strikingly different to the *Pinus cembra* aspect data from the CBNA database for forest stands below
165 2800 m with the main aspect in the Queyras and French Alps mostly north-facing (Fig. 3b).

166 Spatial pattern and physiognomy

167 Pines generally grew in stands consisting of a few up to tens of individuals. They often grew in
168 disconnected stands sometimes hundreds of metres from the nearest woodlands in both distance and
169 elevation (Fig. S1). Some stands were connected to lower elevation forests by a narrow corridor of
170 individuals growing among rocks from the forest-limit to the isolated stands.

171 The physiognomy of 465 pines out of 544 were characterized based on photographs. A few were
172 prostrate (18%; Fig. 4ij), but most were dwarf-shaped (40%; Fig. 4a-c) or erect (39%; Fig. 4d-g). A few

173 (3%) were flag-shaped (Fig. 4hk). The median height was 0.7 m, with a range of 0.2 to 3.8 m (Fig. 5).
174 Malformed female cones of *P. cembra* were observed on a few individuals up to 2855 m asl, and male
175 cones up to 2870 m asl (Fig. S2).

176 Discussion

177 We show that *Pinus cembra* can grow at elevations as high as 3200 m asl in the western Alps, which
178 is about 800 m above the regional observed treeline. Although studies have reported pines growing at
179 high elevation in the western Alps (Bono and Barbero 1971; Motta and Nola 2001; André 2016;
180 Carcaillet and Blarquez 2019) and central Alps (Paulsen et al. 2000; Körner 2012), they have never
181 reported such pine prevalence at exceptional elevations. The peculiar topographic situation of these
182 pine stands, often disconnected from the main range of pines by 400-800 m elevation, recalls that of
183 trees growing on isolated mountains in Arizona, popularized under the metaphor of “sky islands”
184 (Heald 1967). We hereafter discuss the ecological context of these sky island pines and put into
185 perspective their habitats with a history of land use.

186 Trees in cliffs or steep and rocky slopes

187 The observed pines exclusively occur on rocky outcrops, steep slopes, cliffs and ridges (Fig. 4). Such
188 inhospitable habitats raise questions about pine nutrition, because of the limited water storage
189 capacity and nutrient supply. Soil moisture depends on precipitation, but gravity rapidly drains water.
190 Significant cloudiness on summits during the growing season provides moisture in the form of vapor,
191 in the study area notably from humid and warm easterlies coming from the Po River plain. However,
192 pines need mycorrhiza to capture this moisture, as well as to recycle nutrients (Smith and Read 2008).
193 Fortunately, ectomycorrhization seems not to be affected by elevation and, may help in securing pine
194 nutrition (Merges et al. 2018), although access to nitrogen may be limiting.

195 Elevation is a strong driver of pine distribution. The negative exponential model of pine density
196 indicates that survival depends on elevation (Fig. 2), probably regulated by constant mortality or
197 regeneration (Hett and Loucks 1976). The dispersal of *P. cembra* seeds depends on nutcrackers, which
198 preferentially cache seeds in dry soil, but there is a low probability of seedling establishment in dry
199 habitats (Neuschulz et al. 2015). Above 2800 m on steep slopes and cliffs, the habitat is dry and far
200 from seed sources, thus unfavourable for seedlings, especially on south-facing slopes, which undergo
201 severe evapotranspiration due too strong solar irradiance and low-temperature photoinhibition
202 (Germino and Smith 1999). However, east-facing slopes, where 95% of pines are located (Fig. 3b), are
203 more humid thanks to higher cloud-based moisture and lower irradiance. Above 2960 m, most pines
204 growth on south-facing slopes that are warmer (Fig. 3b), perhaps to compensate for the shorter
205 growing season due to higher elevation.

206 **Growth forms: stress and disturbances**

207 The growth form of sky island pines mostly corresponds to a dwarf or prostrate stature (58%), which
208 is an advantage in a cold environment by decoupling the atmospheric temperature from their own
209 under the canopy close to or connected to the ground (Körner 2012). Similar observations of
210 decreasing pine height with elevation indicated a reduced length of annual shoots in similar
211 environments prone to strong wind and low temperature (Takahashi and Yoshida 2009). We also
212 found that needles of pines above 2800 m were smaller than those from forest trees (about 4 cm vs
213 10-12 cm; Fig. S2). The observed reduced leaf length, shoot length, radial growth (Fig. S5), and
214 individual height (Fig. 5) appear to be morphological plasticity in response to abiotic stresses
215 (Schoettle 1990; Kajimoto 1993), notably due to difficulties with building cells and tissues (Rossi et al.
216 2007).

217 While 39% of pines were erect, almost all were damaged by wind, snow, rockfall, or lightning (Fig. 4).
218 These local peculiarities lead to the question of why only erect trees above a certain height are
219 considered to determine treeline, since size is partly controlled by severe disturbances at these
220 elevations. Pine height decreasing with elevation (Fig. 5) is of course partly due to physiological
221 impediments to producing erect stems (Körner 2012) but is also due to disturbances that break stems.
222 The small physiognomy of sky island trees must be considered as a result of the combination of stress
223 and disturbances.

224 **Past land uses: a driver of this species line**

225 The localisation of these elevated rocky and grass-free habitats of isolated pines strongly argues for
226 introduced livestock grazing as the chief mechanism to exclude tree species from alpine grasslands
227 (Fig. S6). Livestock, which do not feed in rocky habitats, control seedlings through grazing and
228 trampling, and saplings and small trees by browsing. Wild herbivores are marginally involved because
229 they naturally have low-density populations.

230 Soil charcoal studies have revealed that pines and larches burned where grasslands occur today,
231 suggesting tree suppression above 2400 m for the needs of animal husbandry. Regionally, burning
232 above 2400 m occurred chiefly between 5000 and 500 years ago (Saulnier et al 2015), with fire
233 frequency peaking about 3500 years ago (Carcaillet and Blarquez 2017). Even though all evidence of
234 past fires shows they were below 2800 m asl, we assume that past livestock grazing combined with
235 anthropic fires explain the scattered distribution of pines above 2400 m or, more often, their total
236 extinction in many alpine areas.

237 **Species line of *Pinus cembra***

238 *Pinus cembra* are growing up to 800 m above the regional treeline (Fig. S7), an observation which
239 appears largely new to the literature, and may be considered as the limit of the fundamental niche of
240 the species. These extreme elevations in the Alps up to 3200 m asl, are perhaps facilitated by the
241 southern location of the study area compared to northern and western massifs that are colder and
242 wetter. One high-elevation occurrence of *P. cembra* has been reported in the central Swiss Alps, up to
243 700 m above the classic treeline, which would be at 3050 m asl (C. Körner, pers. com.). Such
244 observations of isolated elevated pines have largely been overlooked due to a lack of botanical
245 prospecting in harsh, poorly accessible areas with steep cliffs that often prevail in these high
246 mountains (Boucher et al. 2021).

247 **Conclusion**

248 The occurrence of Arolla pines up to 3200 m asl in the Alps is a significant finding that questions their
249 biology and ecology facing ongoing global changes, but also those of the past. First, it is obvious that
250 their ages and their establishment chronology must be studied. The age structure inferred from
251 dendrochronology would provide a net demographic result helpful to explore (i) the balance between
252 mortality and regeneration thanks to demographic hypotheses (Hett and Loucks 1976) and, (ii) the
253 function of past climate and land use drivers by comparison of the age structure with temporal and
254 spatial high-resolution climate reconstructions (<https://climexp.knmi.nl/>) and local domestic
255 husbandry reports (eg, Fortuny et al. 2014). However, sampling problems of small and fragile
256 individuals must be first resolved, as well as counting problems of incomplete tree-rings (eg, Mathaux
257 et al. 2016). Second, this high elevation population questions its genetic origin knowing that glacial
258 refugia of *P. cembra* were found in the same area (Carcaillet and Blarquez 2017), and that present-day
259 population genetics have shown that Arolla pine living in local subalpine forests belong to the most
260 common lineage of western Alps (Toth et al. 2020). We hypothesize (Fig. 6) that this sky-island pines
261 could be relicts of a glacial population, which would have moved in high elevation due their adaptation
262 to peri-glacial conditions, and because forest elevations were better used by more competitive trees,
263 which would have survived to the glacial times near north Italian plain where refugia were evidenced
264 (Vescovi et al. 2007). Such hypothesis would need genotyping of modern populations with best
265 sequencing methods and microsatellite development (Lepais et al 2020), completed by high-
266 throughput sequencing of ancient DNA extracted from subfossil needles to get species genetic
267 chronicles since glacial times (eg, Wagner et al. 2023).

268

269 **Acknowledgements**

270 The authors are indebted to Luc Garraud of the CBNA for his help with the CBNA plant database. We
271 thank Christian Körner for his relevant and valuable advice on a previous version. Chris Carcaillet is
272 indebted to Churchill College in Cambridge and the French Embassy in London for their support as By-
273 Fellow during the writing of the article.

274 **Funding**

275 The research was partly funded by the ANR project Origin-Alps (ANR-16-CE93-0004) and the Labex
276 OSUG@2020 (ANR-10-LABX56). The study contributes to the Long-Term Socio-Ecological Research
277 (LTSER) *Zone Atelier Alpes*, a member of the eLTER-Europe network.

278 **Compliance with ethical standards**

279 **Conflict of interest.** The authors have no conflict of interest to declare. Part of the data used in this
280 article has already been used in a previous article published in a French regional naturalist journal
281 (André 2016). However, the scientific findings and the analysis presented here have not been
282 published and are not under consideration for publication elsewhere. All the authors have approved
283 this submission and all people entitled to authorship have been named.

284 **Authors contribution.** AG carried out the fieldwork and collected most of the data. CC produced a
285 draught of the manuscript, and all co-authors contributed to further versions. All authors approved
286 the final version.

287

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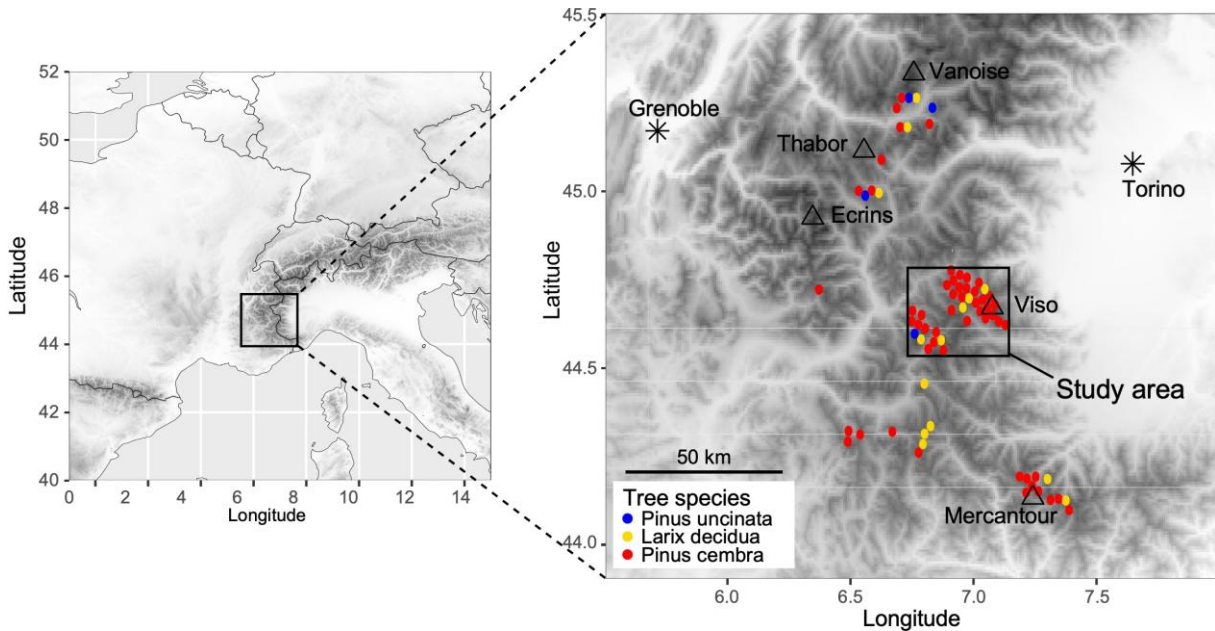
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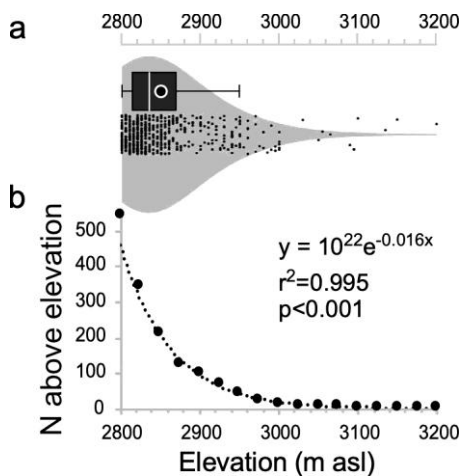
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433 **Figure captions**

434 **Fig. 1.** Study area in the southwestern Alps straddling France and Italy; the small box that delineates
 435 the study area is detailed in Supplementary Information using a topographical map 1/25 0000 (Fig.
 436 S1). The map illustrates the maximal elevations of isolated *Larix decidua*, *Pinus cembra*, and *Pinus*
 437 *uncinata* we observed in the southwestern Alps; only individuals above the classic treeline were
 438 recorded; names of main massifs evoked in the text are indicated.

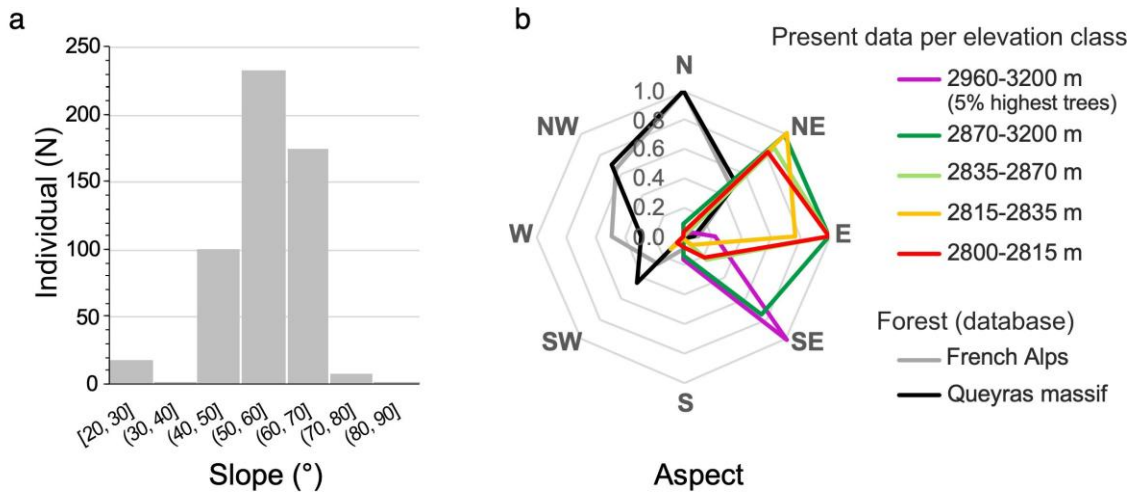


439 **Fig. 2. (a)** Elevation distribution of *Pinus cembra* from 2800 to 3200 m asl illustrated by box-plot and
 440 violin-plot; box-plot: the white circle represents the mean value, the black rectangle is the
 441 interquartile range with the median value (white line), and the whiskers correspond to 1.5x the upper
 442 or lower inter-quartile values; violin-plot: the envelope is a kernel density estimation of the pine
 443 distribution illustrated by small black dots. **(b)** Exponential distribution of number of individuals (N)
 444 above the 25-m elevation class.
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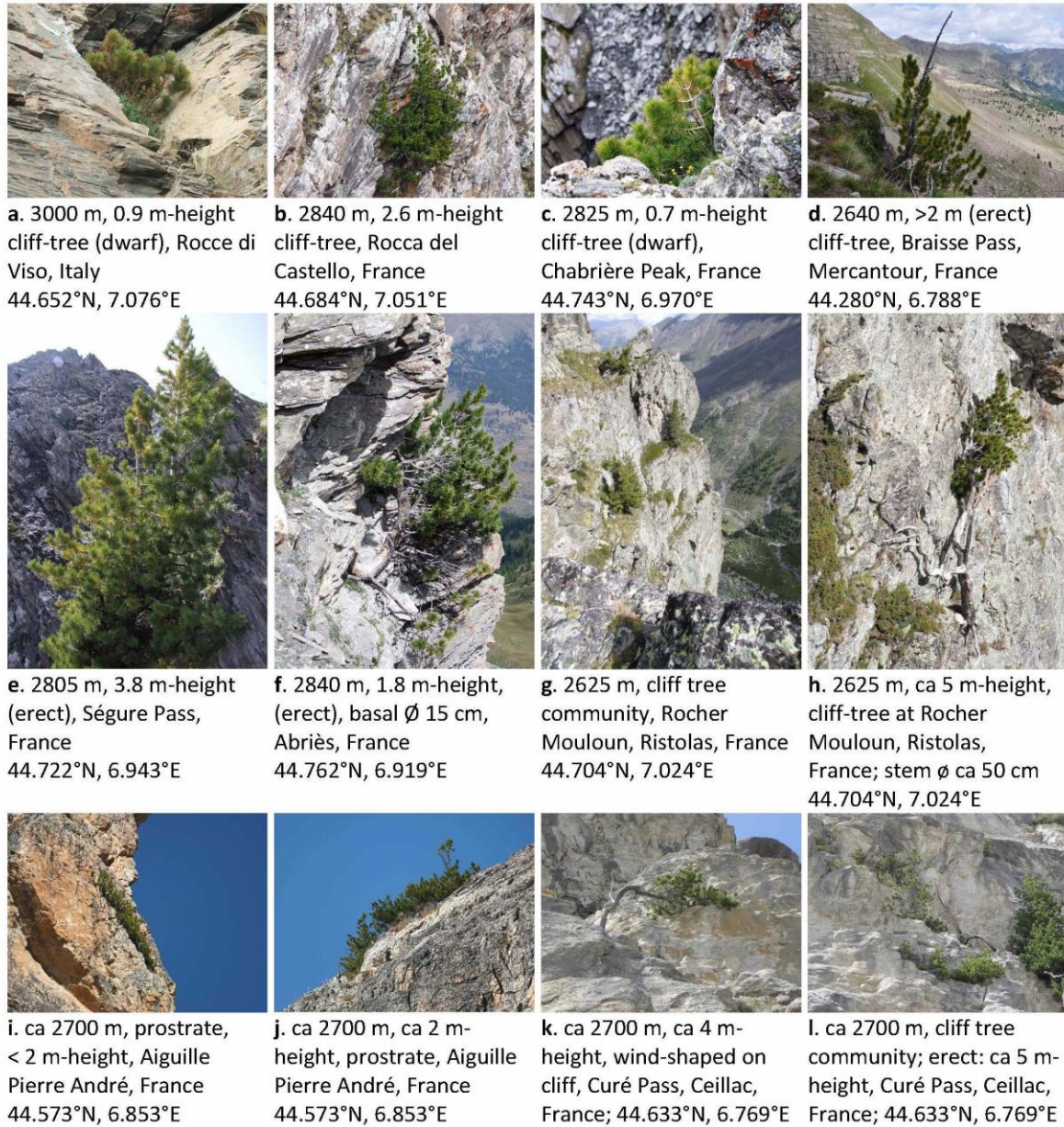


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447 **Fig. 3.** Slope (a) and aspect (b) patterns of *P. cembra* distribution in the Queyras-Viso ecoregion,
 448 western Alps. The data for isolated *P. cembra* (n = 544) above 2800 m are sorted per elevation class
 449 (red, yellow, green, and purple perimeters) and are compared to values for *P. cembra* stands mostly in
 450 lower elevation forests of the Queyras massif (black perimeter) and from the French Alps (grey)
 451 (n = 1747). To compensate for differences in observation numbers, densities were minimax-rescaled
 452 from 0 to 1 by subtracting the minimum numbers per elevation class and dividing by the range of
 453 values of this class. The 95th centile represents the highest 5% of all the elevations where pines were
 454 found.

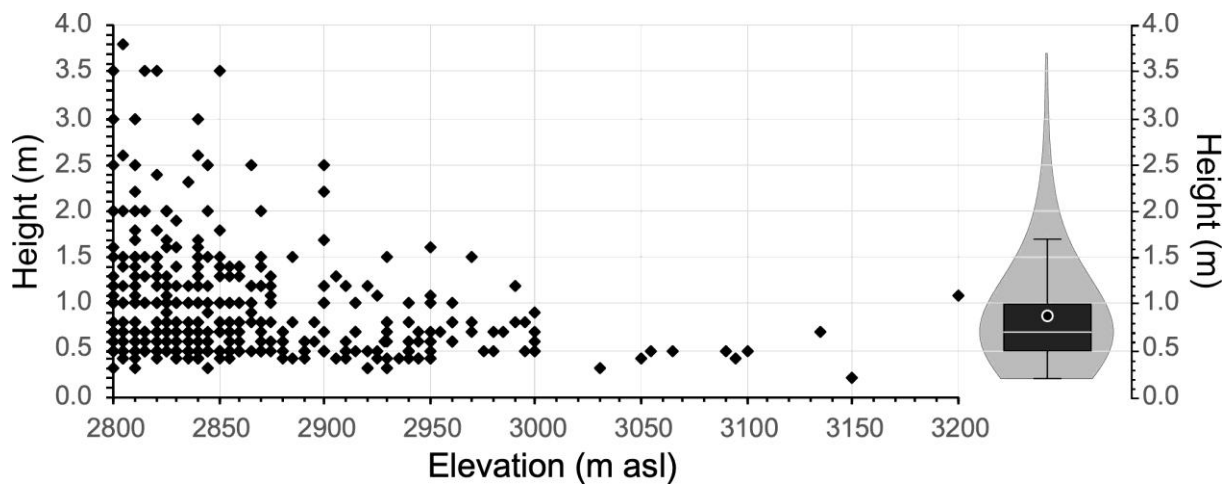


455 **Fig. 4.** Examples of *Pinus cembra* growth forms between 2600 and 3200 m asl in the western Alps, in
 456 France and Italy. These examples illustrate different contexts of growth (cliff, outcrop) on different
 457 rock types (ophiolite [g,h], quartzite [i,j], limestone [k,l], calcareous sandstone [d]), and of pine
 458 physiognomy (dwarf, erect, prostrate, flag-shaped). All pictures are from GA, except [d] from CC.
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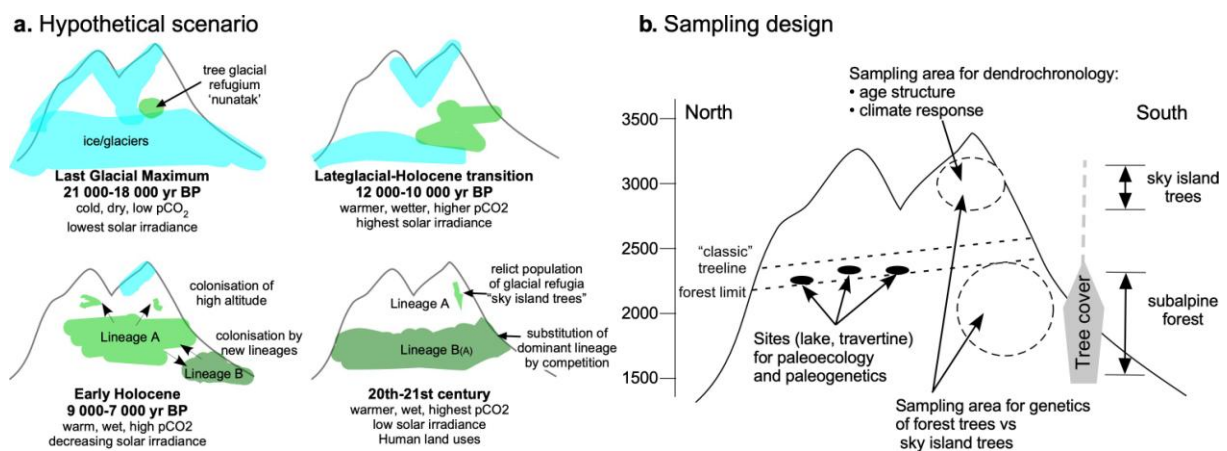
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Fig. 5. Height of *Pinus cembra* plotted against elevation; the median height is 0.7 m, and the 75th percentile is 1.0 m (right: box-plot and violin-plot distribution of heights).



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Fig. 6. (a) Hypothetical scenario of a glacial refugium that would contain a genetic lineage of trees adapted to peri-glacial environmental conditions (climate, soil), which first expanded with the early-Holocene warming and, was confronted with a lineage that was outside the inner Alps during glacial times; here we assume that the colonizing lineage was more competitive than glacial relict lineages; last, due to competition and thanks to adaptation, the glacial relict lineage moves to higher elevation, experiencing harsh conditions similar to those found during glacial times, but in the absence of a more competitive lineage; **(b)** general study design for genetics and paleogenetics, and historical ecology for testing hypotheses of genetic differentiation, population dynamics in response to climate variations.



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